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SHEEP PREDATION BY COYOTES: A BEHAVIORAL ANALYSIS[1]

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Abstract: This paper presents (1) a brief overview of several concepts important to predator-prey behaviors of coyotes, (2) results of an enclosure study of sheep-attack, -immobilization, and -ingestion responses involving 12 male coyotes (*Canis latrans*) that were paired with sheep after observing various sheep-predation events by conspecifics, and (3) an analysis of sheep predation based upon operant learning principles. Contrasts between comparative psychological and ethological approaches to the study of animal behavior are described. Results of the enclosure study (0.127-ha) showed that following matched-length trials of observing predation, non-predation, and lone sheep, 3, 2, and 1 coyote(s), respectively, made fatal attacks (FAs) of sheep. Although a transitive effect occurred for numbers of observer coyotes completing FAs in the 3 groups, the limited sample sizes precluded confirmation of the "observational-learning" hypothesis. Operant learning principles relevant to the predator-prey sequence are discussed.

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Comparative psychology and ethology offer dichotomous approaches to the study of animal behavior. Comparative psychology, with its grounding in American science, focuses upon experimental manipulations designed to highlight species differences in behavior and modes of adaptation, particularly learned adaptations of lower mammals, primates, and humans (Dethier and Stellar, 1961). Ethology, with its European and naturalistic traditions, invokes natural observation to describe behaviors of invertebrate, bird, and some mammalian dyads and social groups; fixed action patterns (FAPs), "releasing" stimuli, and instinctual bases of behavior are emphasized (Dethier and Stellar, 1961).

This report describes a study to assess certain learning effects involved in sheep predation by coyotes. I reasoned that coyotes which observe sheep predation by conspecifics should attack these prey more readily and more often relative to coyotes exposed to models of non-predation or lone sheep.

The influence of observational learning (enhanced acquisition or performance of behaviors via observation of conspecifics) on the predatory behavior of wild canids is well documented (e.g., Adler and Adler, 1977; Connolly et al., 1976; Curio, 1976; Fox, 1969, 1975; Kleiman and Eisenberg, 1973; Mech, 1970; van Lawick and van Lawick-Goodall, 1971; Vincent and Bekoff, 1978). For example, Connolly et al. (1976), in a study of coyote-sheep predation, mentioned that pairing

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0:38 to 19:08) and 1:00 min:sec (range 0:24 to 1:48) for the first and second demonstration trials, respectively (Table 2). Median duration of FA was 8:03 min:sec (range 3:52 to 16:09) and 8:01 min:sec (range 5:52 to 11:06) for these first and second trials, respectively (Table 2). Latencies to FAs were shorter during the second demonstrations; whereas, median lengths of FA were similar for both demonstrations, but had sizable ranges.

Effects of predation observations

A transitive effect occurred among numbers of coyotes that made FAs following demonstrations of predation, non-predation, and lone-sheep -- Group I, 3 > Group II, 2 > Group III, 1 (Table 3). Nevertheless, the Kruskal-Wallis Test showed no differences among Groups for predation variables: (1) number of 1-h trials preceding 3 FAs or 30 days (H = 2.49, NS), (2) cumulative attack durations for the 3 FAs of coyotes exposed to sheep-predation demonstrations (H = 1.23, NS), and (3) number of attacks preceding 3 FAs or 30 days without FA (H = 2.58, NS). Thus, coyotes observing sheep predation by conspecifics failed to reduce the number of trials and attack durations or increase the number of attacks relative to coyotes that observed no predation or lone sheep.

Table 2. Latency to fatal attack (FA) and durations of trials for demonstrator coyotes which determined trial lengths used for coyotes in Groups II and III

			Attack measurements		
Demonstration trial	Demonstrator coyote	Test coyote	Latency to FA (min:sec)	Duration of FA (min:sec)	Trial lengths (min)
1st	A	1	0:38	16:09	32
		2	19:08	3:52	38
	B	3	19:01	11:57	46
		4	12:42	4:49	33
2nd	A	1	1:03	7:35	24
		2	1:48	5:52	23
	B	3	1:00	9:08	25
		4	0:24	11:06	26

Table 3. Sheep-attack/fatal attack (FA) measurements for Group I, II, and III Coyotes during sheep-predation assessments

		Attack measures			
Group	Coyote	Number of coyotes making fatal attack (FA)[1]	1-h trials preceding criterion[2]	Number of attacks	Cumulative duration of 3 FAs (min:sec)
I	1		9	3	25:52
	2	3:4	22	3	20:43
	3		22	11	26:18
	4		30	1	NFA[3]
II	5[4]		21	7	22:53
	6	2:4	25	6	29:54
	7		30	1	NFA
	8		30	0	NFA
III	9		23	3	21:32
	10	1:4	30	1	NFA
	11		30	0	NFA
	12		30	0	NFA

[1]FA often involved a series of intermittent attacks; separation of attacks was defined as stopped pursuit and/or baiting of sheep for ≥30 sec.
[2]Number of 1-h daily trials preceding 3 FAs; shown as 30 days if no FA took place.
[3]NFA--No FA during the 30, 1-h/day sheep-predation assessments.
[4]Coyote 5 escaped after the 1st FA. Missing data were estimated using the median trials, attacks, and durations of FA for other predators (1 df was subtracted from respective Kruskal-Wallis Tests).

Coyote weights were not significantly correlated with occurrence or non-occurrence of FAs on sheep (r_{pbi} = -0.33, NS, critical $value_{0.05}$ =0.71), and heavier coyotes were not more likely to engage in predation than lighter coyotes (Table 4).

Neck attacks predominated (13 of 16 FAs; 81%) in FAs made by 6 test coyotes; however, 1 coyote always used body mauls (3 of 16 FAs; 19%). Characteristics of neck attacks and body mauls were described by Sterner and Crane (In review).

Table 4. Median (range) attack, ingestion, and weight measurements for 6 coyotes that fatally attacked sheep during sheep-predation assessments

Measure	Fatal attack (FA)			
	1st	2nd	3rd	Combined
<u>Attack</u>				
1. Number of 1-hr trials preceding or intervening FA	14.5(1-21)	6.0(1-10)	1.0(1-4)	5.0(1-21)
2. Latency to FA (min:sec)	9:34(0:20-24:24)	2:44(0:20-9:15)	6:56(0:05-14:55)	(0:05-24:34)
3. Number of attacks	1.5(1-6)	2.0(1-7)	1.5(1-4)	2.0(1-7)
4. Anatomical site of FA	(Coyotes 1, 2, 3, 5 & 6 made Neck Attacks; #9 attacked Head and Flank--Fed on Sheep Alive)			
5. Number of lost/regained footings (downings)	1(1-3)	1(1-2)	1(1-3)	1(1-3)
6. Duration of FA (min:sec)	10:46(6:47-9:30)	7:51(7:08-13:44)	8:56(3:52-9:00)	7:38(3:52-13:44)
7. Proportion of FA that sheep remained standing	.10(.03-.34)	.13(.04-.17)	.24(.21-35)	.13(.03-.35)
8. Time to first sheep downing (min:sec)	1:10(0:05-2:32)	1:13(0:30-1:43)	1:55(0:51-2:11)	1:11(0:05-2:32)

Ingestion				
1. Anatomical site of feeding	(Hind-rib/hind-flank/fore-thigh junction = 10, neck = 5, fore-rib/fore flank = 4, hind-thigh = 3, head = 1)			
2. Latency to feed (min:sec)	3:30(0:12-6:15)	2:00(0:01-13:00)	1:00(0:01-3:00)	2:00(0:01-13:00)
3. Number of feeding sites	1(1-2)	1(1-2)	1(1-3)	1(1-3)
4. Amount eaten (kg)	0.5(0.5-1.0)	1.0(0.5-1.5)	0.5(0.5-1.0)	0.5(0.5-1.5)
Weights				
1. Coyote (kg)	10.8(9.0-15.5)	10.0(8.5-15.5)	11.3(9.5-15.5)	10.0(8.5-15.5)
2. Sheep (kg)	14.5(12.5-17.0)	15.0(12.5-18.0)	16.5(14.0-17.5)	15.0(12.5-18.0)

Friedman Tests among FA variables yielded significance for 1-hr trials preceding successive FAs ($X_r^2 = 6.75$, $p < 0.05$) and proportion of FAs that sheep remained standing ($X_r^2 = 8.04$, $p < 0.05$) (Table 4). Nonparametric multiple comparisons revealed that the ranked number of 1-hr trials preceding the first FA was significantly greater than the trials intervening the second to third FA (i.e., median trials decreased from 14.5 to 6 to 1 for 1st, 2nd, and 3rd FA). Conversely, the rank of the proportion of FAs that sheep remained standing was greatest during the third FA (i.e., median proportions were .10, .13, and .24 for the 1st, 2nd, and 3rd FA). Latency to FA ($X_r^2 = 0.75$, NS), number of attacks ($X_r^2 = 0.25$, NS), number of lost/regained footings ($X_r^2 = 0.22$, NS), duration of FA ($X_r^2 = 0.33$, NS), and time to first downing ($X_r^2 = 2.22$, NS) were not different among FAs. In short, the number of sheep pairings intervening FAs decreased sharply following an initial FA, but coyote efficiency at downing sheep during FAs failed to improve from the first to third FA.

Sheep-ingestion measurements

All test coyotes that made FAs fed on the sheep. For these 6 coyotes and 18 FAs, feeding sites encompassed 23 singular or joint anatomical locations (Figure 1). The ordered occurrence of these sites were: hind-rib/hind-flank/fore-thigh junction (43%), neck (22%), fore-rib/fore-flank junction (18%), hind thigh (13%), and head (4%). Coyotes feeding at the junction of the hind-rib/hind-flank/fore-thigh typically opened a small wound and ingested mesentery fat and entrails.

No significant differences were detected among 3 FAs of the "killer" coyotes by Friedman Tests for latency to ingestion ($X_r^2 = 1.74$, NS), number of ingestion sites ($X_r^2 = 0.001$, NS), and amount ingested ($X_r^2 = 2.30$, NS). Latencies to ingestion varied greatly post FAs (range 0:01 to 13:00 min:sec), but median latencies were similar (range 1:00 to 3:30 min:sec) among the successive FAs. Additionally, numbers of ingestion sites and amounts of mutton ingested were not useful variables for documenting feeding efficiency because of restricted variation and insufficient ranges during the feeding period.

DISCUSSION

Analysis of the behaviors displayed during coyote FAs of sheep in the current study seem to best fit operant conditioning principles (see Figure 2). That is, coyote detection, pursuit, attack, injury, immobilization, and ingestion of sheep can be likened to a typical operant chain (Stimulus_0 -- Response_0, S_1 -- R_1, S_2 -- S_2, ... S_x -- R_x), with release of the sheep into the enclosure serving as the S^d (discriminative stimulus) for reinforcement (food). Similar to findings of Sterner and Crane (In review), coyote predation behaviors in this study became more predictable after ≥2 FAs occurred; FAs occurred at increasingly more frequent intervals following an initial FA -- implying significant habituation or learning.

Adler (1955) stated that the success of observational learning is contingent upon the degree to which observed behaviors, or similar behaviors, exist in the animal's response repertoire. To the extent that similar behaviors have been practiced, enhancement of performance due to observations of conspecifics' behavior will be increased. This logic suggests several possible explanations for the current findings. First, we used wild-caught coyotes, with unknown sheep-predation histories. Future comparisons of observational-learning effects in coyotes should involve coyotes with known predation histories, preferably comparisons involving both pen-reared and wild-caught coyotes. Second, my findings agree with a number of earlier studies which have documented the complexities of predator-prey interactions (Adamec et al., 1980; Adler, 1955; Caro, 1980; Vincent and Bekoff, 1978). Observations of predator-prey interactions by conspecifics may not affect the incidence of predation directly in observers; rather, differences may occur for such variables as ontogenetic onset of behaviors and for size/species of prey.

Although a transitive effect for numbers of coyotes making FAs following Group I, II, and III exposures occurred, exposure of wild-caught coyotes to these demonstrations yielded no significant statistical effects upon the initiation or frequency of predation events. Larger sample sizes and the use of both wild-caught and pen-reared coyotes are needed to fully assess the Observational Learning Hypothesis in this context.

Finally, coyotes fed on sheep most frequently at the rib-flank-thigh junction. Whether this reflects nutritional selection by coyotes for the caloric content of mesentery fat, or some other dietary preference, remains unanswered. Still, the research and development implication of this result for coyote management suggests that components of entrails or mesentery warrant examination as possible olfactory/gustatory attractants for coyotes.

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Figure 1. (1a) Terms for Carcass Areas of Sheep Used in Sheep-grading Events (Ensminger, 1970). (1b) Approximate Locations/sizes of Feeding Sites Made by Each Coyote During Predation.

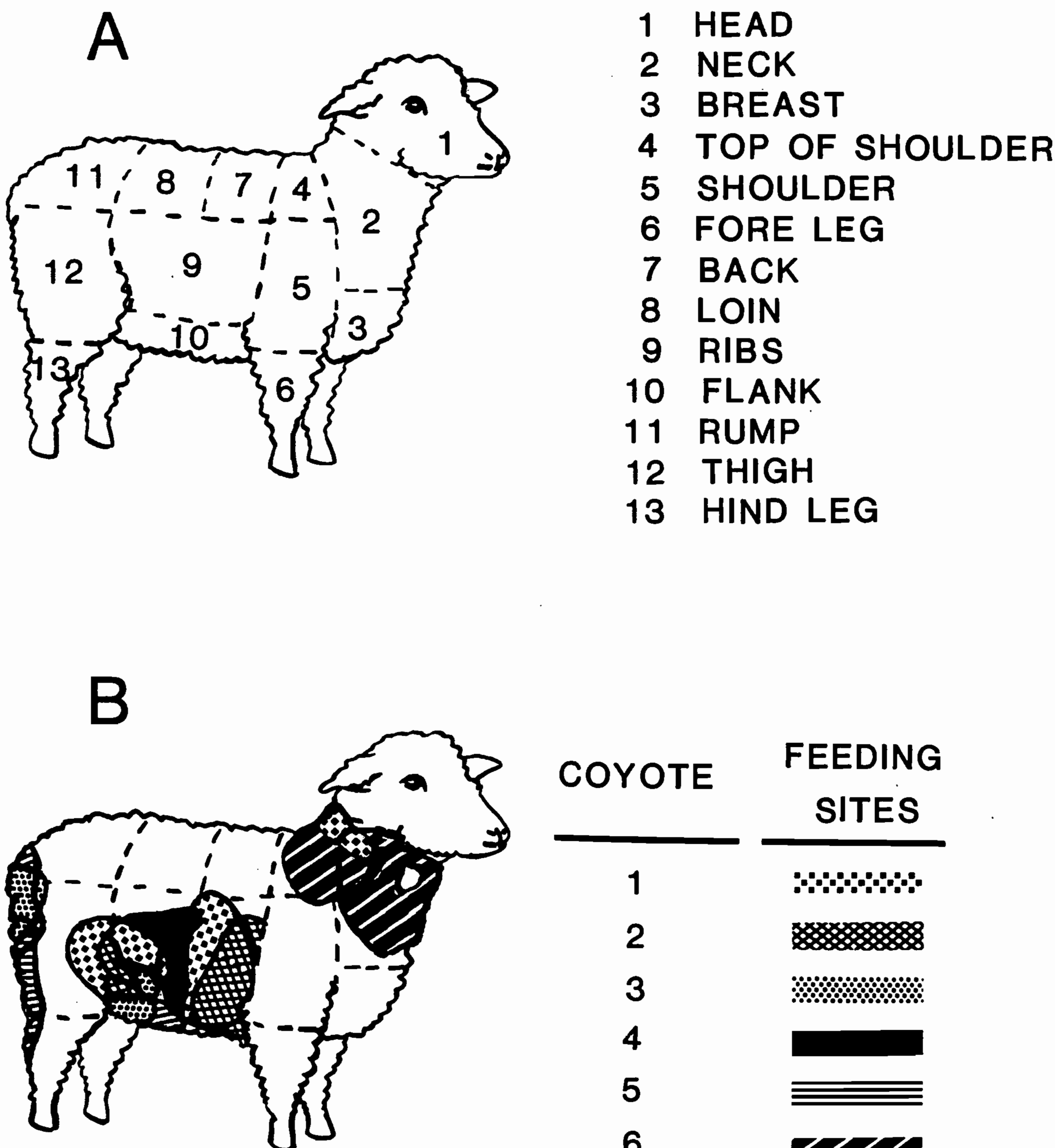

Figure 2. Schematic of a Predator-prey Sequence for Coyote Fas of Sheep (Top) and a Typical Operant Conditioning, Stimulus-response Sequence (Bottom).